Quantitative Assessment of Sea Otter Benthic Prey Communities within the Olympic Coast National Marine Sanctuary: 1999 Re-survey of 1995 and 1985 Monitoring Stations

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Abstract

This report summarizes the changes in the distribution and abundance of selected benthic species within sea otter (*Enhydra lutris*) prey communities along the Washington State Olympic coast between 1987 and 1999. During this 12-year period, the Washington otter population has undergone a dramatic increase in both numbers and range, now occupying habitats that were otter free when first sampled in 1987. Quantitative video and *in situ* counts of invertebrate prey and algal cover at monitoring sites established along the coast in 1987, 1995, and 1999 reveal significant changes occurring as sea otters expanded their range into previously unexploited habitats. Invertebrate prey such as commercially harvested sea urchins that were abundant just outside the boundaries of the 1987 sea otter range are now virtually absent along the entire outer rocky coast. Understory foliose red, coralline, and brown algal cover have also undergone changes as otters removed large invertebrate grazers from the newly occupied habitats.

Introduction

Sea otters (*Enhydra lutris*) were re-introduced to the Washington coast from Alaska during 1969 through 1970. Since that time, particularly over the last decade, the sea otter population has expanded dramatically, from the initial translocation of 59 individuals (Jameson and others 1982), to 100 animals in 1987 (Bowlby and others 1988), >300 in 1995 (Jameson, pers. com, National Biological Survey), and 605 in 1999 (Jameson and Jefferies, 1999). One of the most widely cited examples of the keystone predator hypothesis in community ecology is the sea otter/urchin/algal paradigm, wherein algal communities flourish in areas occupied by sea otters because of reduced grazing pressure due to otter predation on dominant consumers (see Estes and Duggins 1995). This paradigm has emerged primarily from the published results of studies done in Alaskan rocky habitats (Estes and Duggins 1995) but also in southern California (Ebling and Laur 1988). Our study assesses the geographic generality of the trophic cascade from otters to urchins to algae, by examining community changes associated with the expansion of the more southerly and isolated sea otter population along the outer Olympic Coast of Washington State during the period from 1987 to 1999.

Our initial survey of the benthic communities and sea otter habitats along the Olympic coast in 1987 (Kyitek and others 1989) was a typical "space-for-time" test of the sea otter/urchin/algal paradigm. The results of that study revealed low invertebrate prey numbers and biomass within the sea otters' primary range (mean otters sighted/region/aerial survey > 3, after Bowlby and others 1988), somewhat higher numbers within the secondary range (mean otters sighted/region/aerial survey < 3, after Bowlby and others 1988), and much higher levels of prey resources outside the range, especially to the north (Figures 1 and 2a). Abundance of foliose red algal species palatable to sea urchins was positively correlated with sea otter abundance (Figure 3) (Kvitek and others 1989). Based on those results, we predicted that as the Washington State sea otter population continued to grow, it would most likely expand to the north, drawn by and depleting the rich prey resources found there. We also predicted that if sea otters did move into these northern habitats, there would be significant changes in the benthic algal cover if the otters did reduce the abundance of sea urchins and other invertebrate grazers as expected. Finally, we predicted that sea otters would be slower to colonize, and prey biomass would be higher following range expansion, at sites with the highest water velocities, such as those at the mouth of the Strait of Juan de Fuca. Current speed and other physical impediments to sea otter foraging efficiency have been shown to influence sea otter foraging site selection in soft-bottom prey communities (Kvitek and others 1992, Kvitek and others 1988).

Puget Sound Research 2001

The 1987 study established the baseline necessary for a direct test of these sea otter community effects at some point in the future if and when the Washington State otter population expanded its range. In the summer of 1995 we conducted a resurvey of the 1987 sites, and expanded the number of sites and depths sampled including sites at the mouth of the Straits of Juan de Fuca (Tatoosh Island and Cape Flattery) (Kvitek and others 1997, 1998). By 1995, sites previously unoccupied or sparsely populated by sea otters in 1987 (Bowlby and others 1988; Kvitek and others 1989) were all occupied by much higher numbers of sea otters, and otters were now regularly seen at Cape Flattery and Tatoosh Island (Figures 1 and 2b). Significant decreases in prey abundance and biomass (primarily sea urchins and sea cucumbers) were found at all resampled sites. High numbers of large sea urchins were only found in the highly exposed, current swept sites at Cape Flattery and Tatoosh Island. Palatable algal abundance (foliose red algae) increased significantly where measured at sites recently occupied by sea otters, but less palatable coralline algae decreased in abundance at the site experiencing the most dramatic decline in sea urchin prey.

Here we report the results from our June 1 through 12, 1999 resurvey of the 1987 and 1995 study sites. Our goal was to see if the invertebrate and algal trends seen in 1995 were continuing with the growth of the Washington sea otter population. Of particular interest was whether or not the remnant population of abundant large sea urchins found in 1995 in the high current areas of Cape Flattery and Tatoosh Island were still intact after several years of otter occupancy.

Methods

Current sea otter distribution and abundance data was obtained from the National Biological Service Washington State census (Jameson and Jefferies, 1999, unpublished data). Video quadrat techniques were used to resample 8 shallow subtidal survey sites originally established along the Olympic coast during August of 1987 (Figure 1; Kvitek and others 1989), and the additional sites added in 1995 (Kvitek and



others 1997). The original methods employed in 1987 consisted of divers counting and measuring invertebrates and percent algal cover within 1m² quadrats deployed along 10 meter transect lines. For the 1995 and 1999 surveys conducted aboard the R/V *Tatoosh*, these methods were updated to increase sampling efficiency through the use of quantitative video sampling techniques. This method utilized a Sony Hi8 video camera in a light-equipped Light and Motion Stingray® housing fitted with two forward facing PVC pods. These pods were of appropriate length and position such that when the diver/operator

positioned the camera to point vertically down at the sea floor while resting on the pod ends, the video field of view was $0.25~\text{m}^2$ and the pods were outside the field of view. The operator was thus able to move across the seafloor with the camera running continuously, pausing momentarily to push the pods against the substrate, capturing $0.25~\text{m}^2$ video images for later analysis. To aid in the later measuring of individuals on the video display, the operator placed a 20 cm long scale bar in the field of view of the beginning and ending frames of each quadrat series.

The divers captured the video quadrats along continuous transects, in an effort to duplicate as closely as possible the techniques employed during the 1987 survey. The limits of video resolution required that a smaller quadrat size be used than the 1-m^2 in situ quadrats used in 1987. However, a test comparison at a nearby survey site in 1995 (Chibahdehl Rocks) of invertebrate size and abundance data collected using both methods showed no significant difference in results (t-tests, p = 0.32 and 0.24 for abundance and size, respectively). Power was not optimal but reasonably high for both of these comparison t-tests as well (power = 0.66 for abundance t-test, 0.67 for size t-test). Chibahdehl Rocks was chosen for this comparison because prey, although rare, was sufficiently abundant there to allow evaluation of both size and abundance efficiency for each method (although rarity and high variability of prey probably lowered the power of our method comparisons). For these reasons, we have relied entirely on video data for the remainder of the study. Our confidence in the results from this method increased with our qualitative observations of the obvious and dramatic decrease in sea otter invertebrate prey abundance at all sites since 1987.

In addition to the video quadrats, divers in 1999 also counted and measured invertebrates *in situ* along haphazardly placed transects that were either 25 x 1 m or 25 x 2 m depending on invertebrate density.

These transects were used to both validate the video data and to address the problem of very low invertebrate density when trying to get enough individuals for a size distribution estimate.

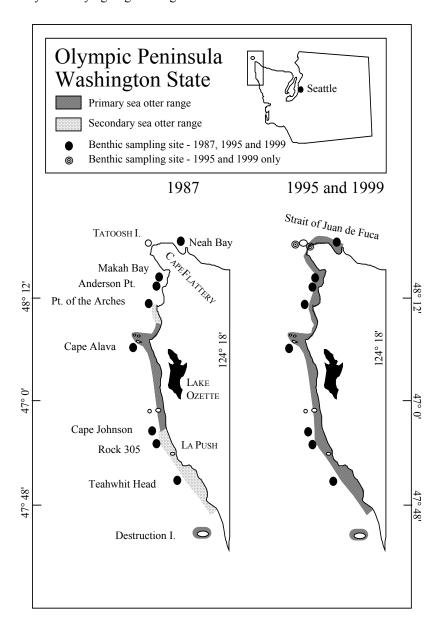


Figure 1. Benthic sampling sites and the sea otter ranges for 1987, 1995 and 1999 along the Olympic coast of Washington State. Methods and data for determining primary otter range (> 3 otters observed per survey) and secondary otter range (<1 otter observed per survey) come from Bowlby and otherss 1988, and Jameson National Biological Survey unpublished data.

Videotapes were viewed in the laboratory, where benthic invertebrate species were identified, counted, and measured within each 0.25-m^2 video quadrat for all sites. Invertebrate prey biomass was determined based on size/weight regression formulae derived during the 1987 project (Kvitek and others 1989). Only conspicuous, exposed otter prey items were counted, as divers did not overturn rocks or otherwise disturb the substrate when quadrats were recorded in the field. For this reason, extremely cryptic or hidden otter prey such as octopus and crabs may have been overlooked by our methods [this may account for the

Puget Sound Research 2001

apparent paradox of increased otter numbers yet low prey at Cape Johnson, Rock 305, and Teawhit Head in 1995 (Figure 2b)]. Stacking or layering of prey did not occur in any quadrats recorded. Percent cover of substrate type was determined from 0.25-m² video quadrat frames by superimposing a random pattern of 50 dots on the image; layering was not accounted for, as only the uppermost visible substrate type was recorded.

Statistical comparisons of all three sampling years were run using the Kruskal-Wallis test. The Mann-Whitney test was used to test for significant changes occurring between 1995 and 1999, and Kruskal-Wallis tests were used for between site comparisons.

Results

In 1987, prey abundance and biomass were inversely proportional to sea otter abundance (Figure 2a). By 1995, prey abundance and biomass remained low at the 1987 sea otter sites, and had declined dramatically at previously sampled sites recently invaded by sea otters (Figure 2b, Table 1). In 1995 Sea urchins had become rare or absent at all sites within the otter range, with one very notable exception, the highly exposed and current swept mouth of the Straits of Juan de Fuca (Figure 2b). Here, Tatoosh Island and Cape Flattery both supported urchin numbers and biomass dramatically and significantly higher than at any other location (Kruskal-Wallis test, $p \le 0.0005$). By 1999, however, these last remaining pockets of high prey biomass within the otter range were gone (Figure 2c, Table 1). In fact, we witnessed the removal of the final patch of large urchins by an otter at Tatoosh just before running the video quadrats that year. For 1999, there was no significant difference in prey abundance between sites.

Foliose red, coralline and brown algal cover were measured at three sites, Neah Bay, Anderson Pt. and Cape Alava for all years (Figure 3). Foliose red algal cover at Neah Bay has increased significantly from 0% in 1987 to 24% and 15% in 1995 and 1999 respectively (Kruskal-Wallis, p < 0.0001), while decreasing significantly at Anderson Pt. (Kruskal-Wallis, p < 0.0001), and dropping at Cape Alava (Kruskal-Wallis, p = 0.0; Figure 3a). The only significant difference in foliose red cover between 1995 and 1999 was the decline at Anderson Pt. (Mann-Whitney U-test, p < 0.0001). Coralline cover continued to drop dramatically and significantly at Neah Bay (100%, 44%, 1%; Kruskal-Wallis, p < 0.0001, Mann-Whitney U-test p < 0.0001), and at Anderson Pt. (18%, 17%, 6%; Kruskal-Wallis, p = 0.001, Mann-Whitney U-test p < 0.0001), while fluctuating slightly but significantly at Cape Alava (Kruskal-Wallis p = 0.001, Mann-Whitney U-test, p = 0.0006; Figure 3b). Brown algae has increased steadily and significantly from 0 to 33% at Neah Bay since 1987 (Kruskall-Wallis p < 0.0001, Mann-Whitney U-test p = 0.009), fluctuated significantly between 4% and 34% at Anderson Point (Kruskall-Wallis p < 0.0001, Mann-Whitney U-test, p < 0.0001), and did not change significantly at Cape Alava (Kruskall-Wallis p = 0.49, Mann-Whitney U-test, p = 0.20; Figure 3c).

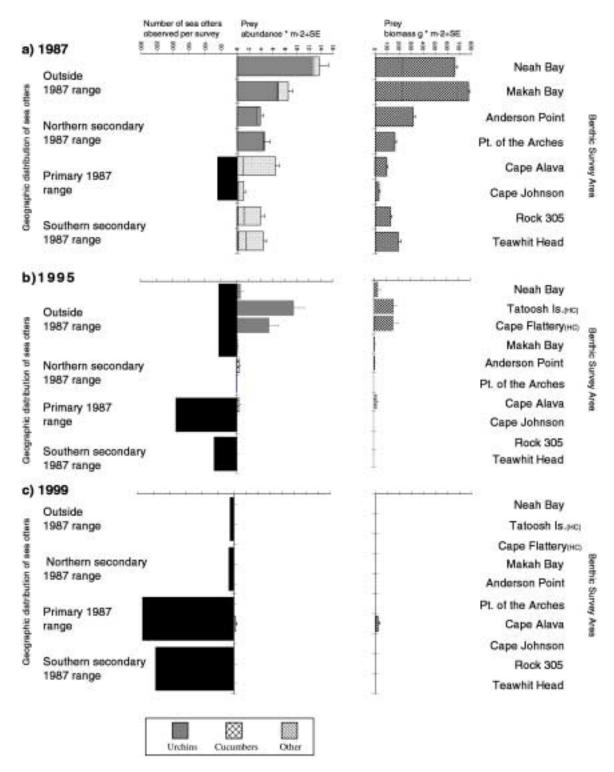


Figure 2. Invertebrate prey abundance at benthic sampling sites for 1987, 1995 and 1999, related to sea otter abundance. HC = high current areas at Tatoosh Island and Cape Flattery. These two sites were sampled in 1995 and 1999 only.

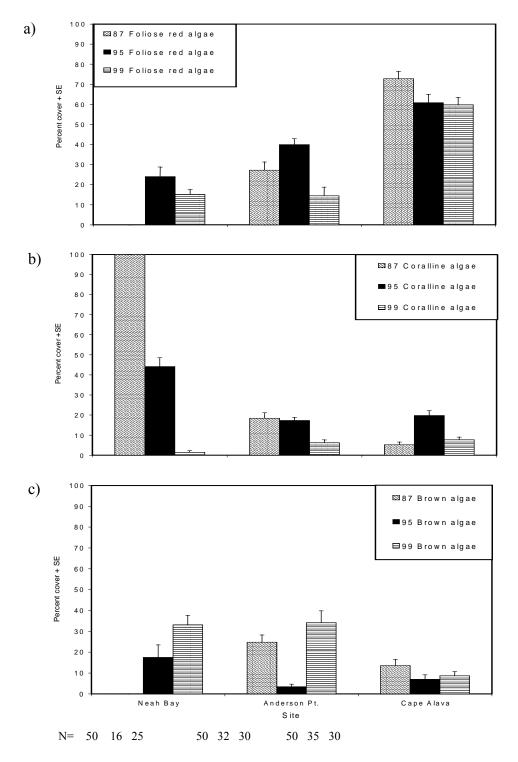


Figure 3. Changes in percent foliose red, coralline and brown algal cover following sea otter expansion from 1987 to 1999. $N = number of 0.25m^2 quadrats$.

Table 1. Total Prey Density and Biomass form Video

Total prey density (#/m²) and biomass (g/m²) at sites for which 1995 and 1999 0.25m² video quadrat data have been collected, extracted, and processed. NS=No samples taken. A=Archived

		1995					1999				
	Depth	Total Prey Density		Total Prey Biomass			Total Prey Density		Total Prey Biomass		
SITE	(m)	n	mean #/m2	(SD)	mean g/m2	(SD)	n	mean #/m2	(SD)	mean g/m2	(SD)
Neah Bay	6	16	0.75	(2.00)	40.03	(160.10)	30	0.00	(0.00)	0.00	(0.00)
Neah Bay	12	NS	NS	NS	NS	NS	30	0.00	(0.00)	0.00	(0.00)
Makah Bay	6	36	0.11	(2.27)	0.00	(0.00)	30	0.00	(0.00)	0.00	(0.00)
Anderson Pt.	6	32	0.50	(0.67)	7.10	(40.16)	30	0.00	(0.00)	0.00	(0.00)
Pt. of the Arches	4.5-6	20	0.00	(0.00)	0.00	(0.00)	30	0.00	(0.00)	0.00	(0.00)
Cape Alava	3-4.5	35	0.46	(2.29)	0.00	(0.00)	30	0.27	(1.02)	23.09	(87.88)
Cape Johnson	4.5-6	31	0.00	(0.00)	0.00	(0.00)	30	0.00	(0.00)	0.00	(0.00)
Rock #305	6	30	0.00	(0.00)	0.00	(0.00)	30	0.00	(0.00)	0.00	(0.00)
Teawhit Head	6-horiz	30	0.00	(0.00)	0.00	(0.00)	30	0.00	(0.00)	0.00	(0.00)
Cape Flattery	6-slope	14	0.13	(0.73)	0.00	(0.00)	30	0.00	(0.00)	0.00	(0.00)
Cape Flattery	12	16	0.25	(1.00)	2.34	(9.34)	30	0.00	(0.00)	0.00	(0.00)
Cape Flattery	18-21	32	6.50	(13.52)	198.81	(370.32)	30	0.00	(0.00)	0.00	(0.00)
Tatoosh Island	6-horiz	13	1.23	(4.44)	14.73	(53.10)	NS	NS	NS	NS	NS
Tatoosh Island	6-slope	27	13.48	(15.98)	207.73	(225.17)	28	0.00	(0.00)	0.00	(0.00)
Tatoosh Island	12	30	35.33	(16.21)	1114.95	(486.83)	32	0.25	(0.98)	6.75	(28.68)
W. Chibahdehl	6	Α	A	A	A	A	30	0.00	(0.00)	0.00	(0.00)
W. Chibahdehl	12	Α	Α	A	A	A	30	0.00	(0.00)	0.00	(0.00)
W. Chibahdehl	18	Α	Α	A	Α	Α	30	0.13	(0.73)	11.55	(63.24)
Umatilla Reef	6	NS	NS	NS	NS	NS	30	0.00	(0.00)	0.00	(0.00)
Umatilla Reef	12	Α	Α	A	Α	A	30	0.13	(0.73)	11.55	(63.24)
Umatilla Reef	18	Α	Α	A	Α	Α	30	0.00	(0.00)	0.00	(0.00)
Perkins Reef	6	Α	A	A	A	A	30	0.00	(0.00)	0.00	(0.00)
Perkins Reef	12	Α	Α	A	Α	Α	25	3.36	(5.12)	188.05	(175.08)
Destruction Island E	6	Α	Α	A	Α	A	30	0.00	(0.00)	0.00	(0.00)
Destruction Island SW	6	Α	A	A	A	A	30	0.13	(0.73)	11.55	(63.24)
Destruction Island SW	12	Α	Α	A	Α	A	30	0.00	(0.00)	0.00	(0.00)

Conclusions

As predicted, while the otters increased in numbers within their range following the 1987 survey, their range also expanded to the north (Figure 1, Jameson, National Biological Service). Coincident with this expansion, prey abundance and biomass declined by an order of magnitude to very low levels at the newly otter-occupied sites on either side of Cape Flattery by 1995 (Figure 2b). By 1999, the high prey numbers and biomass found at Cape Flattery and Tatoosh Island in 1995 had also dropped to levels comparable with the other monitoring sites (Figure 2c, Table 1). The seemingly anomalous persistence of high prey abundance found within the sea otter range in 1995 may have resulted from the expanding otter population skipping over this area due to the typically heavy seas and strong tidal currents found there (Department of Fisheries and Oceans, Canada, 1997, U.S. Department of Commerce, NOAA, USA, 1992). Prior to 1999 sea otters were rarely observed at Tatoosh Island (R. T. Paine, pers. com.). This refuge from otter predation, however, was short-lived. The rich concentrations of sea urchins and other invertebrates found there in 1995 had finally fallen prey to otters by 1999 (R. T. Paine, pers. com. and authors' observations).

Finally, removal of urchin grazers by sea otters was most likely responsible for the rise in cover of more palatable algae at the recently occupied Neah Bay and Anderson Pt. sites (Figure 3, 4, 5). The most dramatic change in algal cover occurred at Neah Bay, the site that experienced the greatest decline in urchin abundance following the movement of sea otters into the area. Prior to otter occupation Neah Bay was dominated by coralline algae, common in urchin barrens, with foliose red and brown algae not present (Figure 3). By 1995, coralline cover had dropped from 100% to 44%, while foliose red and brown algae had both gone from 0% to 24% and 18% respectively. By 1999, coralline cover had dropped to 1%, while foliose reds occupied 15%, and browns increased further to 33% cover. Cape Alava, which experienced the least change in invertebrates having been at the center of the sea otter range the longest, showed the least change in relative abundance of algal cover. Anderson Pt., which also saw a significant drop in urchin numbers following otter range expansion (Figure 2), also showed a drop in coralline cover, with an overall combined increase in the more palatable algal taxa, alternating between red and brown algae during 1995 and 1999.

These results are consistent with and extend the generality of Estes and Duggins (1995) conclusion that where sea otters are established, urchin herbivory will generally not be a dominant force structuring near-shore benthic communities. It is also clear that expansion of the sea otter population, coupled with other factors, has eliminated the potential for commercial harvest of sea urchins along the outer coast of the Olympic Peninsula, and the mouth of the Strait of Juan de Fuca.

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